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Lower Jurassic cockroaches (Insecta: Blattaria) from Germany and England

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ABSTRACT

Types of the Lower Jurassic cockroaches described by Geinitz, Scudder, Handlirsch and Bode from Germany and England are redescribed. Forty-five previously described Lower Toarcian cockroach species are synonymised into six species. The type genera of the Mesoblattinidae (*Mesoblattina* Geinitz, 1880) and Caloblattinidae (*Caloblattina* Handlirsch, 1906) with their type species *Blattina protypa* Geinitz, 1880 and *Blattina mathildae* Geinitz, 1883 are restudied. Redescribed are the holotypes of the Lower Liassic *Mesoblattina geikiei* Scudder, 1886 and the Lower Toarcian *Mesoblattina blakei* Scudder, 1886. The systematic affinity of *Eublattula crassivena* Handlirsch, 1939 is still unresolved. The variability of the 88 studied specimens of the dominant Lower Toarcian cockroach *Blattula langfeldti* (Geinitz, 1880) (Blattulidae) is found to be much greater than the variability of Lower Cretaceous Blattulidae of the same size. Compared with most sites of the Middle–Late Jurassic and Early Cretaceous world-wide, the diversity of the studied Lower Jurassic cockroaches is surprisingly low, probably as a result of destabilised ecosystems of the island source areas.

KEY WORDS: Blattaria, Blattidae, Blattulidae, Caloblattinidae, Mesoblattinidae, cockroaches, Jurassic, Toarcian, England, Germany, revision, new synonymy.

INTRODUCTION

Cockroaches are among the most abundant terrestrial arthropods in the non-marine Late Palaeozoic–Mesozoic fossil record. Thus, in the case of their detailed study they may represent fine evolutionary, not to mention stratigraphical, data. Nevertheless, knowledge of their role in the ecosystems of the past is still scarce.

The present work gives evidence of the necessity for redescription of the earlier-studied type material, after which the extensive cockroach diversity of some Triassic and Early Jurassic sites appears very limited. The cockroach diversity of the European Early Toarcian sites is found to be low, even when compared to most of the Jurassic sites. Nevertheless, the abundance of the most common species reveals useful data on the variability of the wing venation, which highlight some specific aspects of the group in general, such as changes in control mechanisms, variability changes (ecological plasticity of species), etc. (Vršanský 2000). The most fascinating result of the above-mentioned study was, in particular, the decreasing variability of species from the Carboniferous to the present, supported by results of the present study.

The Early Jurassic is rather static with regards to the evolution of the cockroach fauna. Palaeozoic Phyloblattidae and Archimylacrididae as well as Mesozoic groups are present during this time. In the German localities of the Early Toarcian, Mesoblattinidae, Blattulidae, Caloblattinidae and a new family (to be established for *Rhipidoblattina* and related genera on the basis of better and more complete material (Vršanský, in press)) are present in low diversity (five species of 119 studied specimens).

The systematic position of *Eublattula crassivena* Handlirsch, 1939 remains disputable. The material described below is of particular importance, since it comprises the types of Geinitz (1880, 1883, 1884, 1887), Scudder (1886), Handlirsch (1906–08, 1920, 1939) and Bode (1953), including the types of an abundant Mesozoic cockroach family, Caloblattinidae, and Mesoblattinidae. The type of *Mesoblattina protypa* evidently differs from other species placed into Mesoblattinidae in the past. All the known species, except for the type and some additional species, were removed and placed within Caloblattinidae (Vršanský 2000) and in a new family (Vršanský, in press). A number of "mesoblattinids" were previously removed from the Mesoblattinidae to Blattulidae (Vishniakova 1982). The Mesoblattinidae is now found to be restricted to the Jurassic and Early Cretaceous, representing a progressive evolutionary stem, ancestral to modern Blattidae, Blattellidae (Vršanský *et al.* 2002; Vršanský 2002) and probably also Blaberidae. The Mesoblattinidae most probably evolved from the new family, to be established for *Rhipidoblattina* and other genera, or its ancestors during the Late Triassic–Early Jurassic. Finally, the current detailed observations of the cockroach fauna of the Early Cretaceous (Vršanský 1999*a*, *b*, 2000, 2002; Vršanský & Ansorge 2001; Vršanský *et al.* 2001, 2002) allow us to compare some aspects of the Jurassic–Cretaceous stages within the evolution of Blattaria.

LOCALITIES AND MATERIAL

A number of very rich Lower Toarcian (Late Liassic, Early Jurassic) insect localities is known in Europe. These localities are situated in Germany, Luxembourg/Belgium and England (Ansorge 1996, 2003, 2004). All Upper Liassic insects in Europe originate from limestone concretions which are intercalated within Posidonia Shale, except for north-eastern Germany where the concretions were formed in plastic clay of the "Green Series". The insects were buried as a component of a marine taphocoenosis; they are associated with marine molluscs such as ammonites, theutoids, bivalves and gastropods. Fishes and reptiles are also present. Besides driftwood and extremely rare terrestrial reptiles, insects appear to be the most numerous of land inhabitants. Associated ammonites indicate the presence of the *falciferum* Zone, subdivided into the lower *elegantulum* Subzone and the subsequent *exaratum* Subzone.

Cockroaches have been described from several Lower Toarcian localities in Europe. The first cockroaches were described by Geinitz (1880, 1883, 1884, 1887) from Dobbertin in Mecklenburg, Germany. At the same time, Scudder (1886) reported two cockroach species from the Lower Toarcian of Gloucestershire in England. Handlirsch (1906–08, 1920, 1939) restudied the types from Germany and England and added a number of new species from Dobbertin. Bode (1953) described a number of Blattaria from several different localities (Hondelage, Schandelah, Hattorf) in the vicinity of Braunschweig (Brunswick, Lower Saxony, Germany). Almost all of these species were based on the holotypes only. Brachert (1987) mentioned the presence of cockroaches in a temporary outcrop at the Rhine-Main-Donau canal near Kerkhofen in Bavaria (Germany). Berger (1989) figured one species from the same locality. Delsate *et al.* (1992) reported two specimens from the Lower Toarcian Posidonia Shale of Belgium.

In recent years the junior author collected some thousands of fossil insects in the Lower Toarcian of Grimmen (Western Pomerania), Dobbertin (Mecklenburg), Schandelah near Brunswick (Lower Saxony) and Mistelgau near Bayreuth (Bavaria). From his data the following percentages of cockroaches were counted: Grimmen, 2.0% of 2042 insects; Dobbertin, 4.3% of 958 insects; Brunswick, 0.4% of 663 insects; Mistelgau, 1.6% of 176 insects. These percentages are mostly considerably lower than the data from the material studied by Handlirsch (Dobbertin, 7.2%) and Bode (Brunswick, 3.0%). These smaller percentages of cockroaches in the fossil material may be a result of a subjective preference which earlier collectors might have had for larger insects. Cockroaches are also present in the famous Posidonia shales of Holzmaden (*Liadoblattina blakei*) and in the Posidonia shales of Bascharage in Luxembourg (Henrotay *et al.* 1998).

The geographical positions of the mentioned Lower Toarcian localities are as follows: Dobbertin (Mecklenburg) [53°61'50"N:12°11'10"E], Grimmen (Western Pomerania) [54°13'30"N:13°06'00"E], Schandelah (Lower Saxony) [52°28'50"N:10°70'70"E], Mistelgau (Bavaria) [49°28'40"N:11°46'60"E], Kerkhofen (Bavaria) [49°16'20"N:11°39'30"E], Holzmaden (Württemberg) [48°63'50"N:9°52'70"E], Bascharage (Luxembourg) [49°56'20"N:5°91'70"E], Alderton (Gloucestershire) [52°00'N:2°00'W].

About 120 cockroaches, mainly wings, were studied from these localities (Table 1).

The type material is kept in the Institut für Geologische Wissenschaften, der Ernst-Moritz-Arndt Universität Greifswald (FGWG); Roemer-Pelizaeus Museum Hildesheim (Hi); Geologisch-Paläontologisches Institut, TU Clausthal-Zellerfeld (Cl); Geologisch-Paläontologisches Institut der Universität Göttingen (G); Forschungsinstitut Senckenberg, Frankfurt am Main (SNM; W, former Wunnenberg collection; B, former collection of Technische Hochschule Braunschweig); Naturhistorisches Museum, Vienna (NHMW); Natural History Museum, London (NHML). The specimens labelled LGA (Grimmen), LDA (Dobbertin), S (Schandelah), M (Mistelgau) are from the private collection of J. Ansorge, later to be housed at the Museum für Naturkunde der Humboldt Universität, Berlin.

Photographs were taken with a NIKON Coolpix 4500 digital camera, adapted to various optical equipment; drawings are camera-lucida based or re-drawn photographs using ROTRING pens.

Abbreviations used: Fw – forewing; Hw – hindwing; Sc – subcosta; R – radius; RS – radial sector; M – media; CuA – cubitus anterior; CuP – cubitus posterior; A – anal veins.

TABLE 1

Material studied from the German Lower Toarcian localities.

	Dobbertin		Grimmen		Brunswick		Mistelgau		Holzmaden		TOTAL
	Fw	Hw	Fw	Hw	Fw	Hw	Fw	Hw	Fw	Hw	
Blattula langfeldti	32	20	14	18	4	-	-	-	-	-	88
Blattula dubia	-	2	1	-	-	-	-	-	-	-	3
Eublattula crassivena	1	-	-	-	-	-	-	-	-	-	1
Mesoblattina protypa	3	-	2	-	-	-	2	-	-	-	7
Caloblattina mathildae	3	-	-	-	5	2	-	-	-	-	10
Liadoblattina blakei	2	2	-	-	1	3	-		2	-	10
TOTAL	41	24	17	18	10	5	2	0	2	0	119

TAXONOMY

Order Blattaria Latreille, 1810

Superfamily Blattoidea Latreille, 1810

Family Mesoblattinidae Handlirsch, 1906

Type genus: *Mesoblattina* Geinitz, 1880.

Diagnosis: Medium-sized cockroaches, plesiomorphically with short external ovipositor, with generally reduced and regular venation (with exception of area between bases of M and R) without branchlets, and with dense venation present in apical parts of R and M in forewing. Forewings with more or less parallel borders, without distinct intercalaries. A without numerous reticulations; venation of Cu and M, with exception of the first stem, regular; R straight; Sc two- to four-branched. Hindwing with simple Sc; R1 and RS differentiated; M with up to 5 branches; CuA secondarily branched and with additional blind branches; CuP simple.

Composition: *Mesoblattina* Geinitz, 1880; *Hispanoblatta* Martínez-Delclòs, 1993; *Archimesoblatta* Vršanský, 2003; *Praeblattella* Vršanský, 2003; *Breviblattina* Vršanský, 2004; *Mongolblatta* Vršanský, 2004 and a new genus represented by "*Artitocoblatta*" *colominasi* Meunier, 1914.

Remarks: The family represents the most advanced group of Lower Jurassic cockroaches, ancestral to contemporary lineages of Blattidae, Blattellidae and Blaberidae. The latest mesoblattinids share strong synapomorphies with Blattellidae and Blattidae (regular venation; forewing with parallel borders, RS differentiated, simple A; hindwing with simple CuP). Early Blattidae differ only in hindwing M which is branched, and the Mesoblattinidae (*Praeblattella*, *Hispanoblatta,* etc.) in possessing a short, rudimentary external ovipositor (the composition of the terminalia is a diagnostic character for Blattidae and Blattellidae).

The Mesoblattinidae evolved during the earliest Jurassic or possibly earlier (Vršanský 2003) from the stem group including the Caloblattinidae and a new family, or directly from the new family erected for *Rhipidoblattina* and other genera (Vršanský, in press).[*] They are synapomorphic in the hindwing composition with R comb-like, blind branches of CuA and simple CuP. They also share branched Sc in the forewing, some apical branchlets in A, and irregularity of venation (all plesiomorphies). The irregularity of venation is a strong plesiomorphy. The regularity of venation means that the distance between the competent veins is constant (exceptions might be Sc–R and the clavus with its branches, which have both supportive and/or protective functions). This regularity is affected only by the dichotomy and only immediately after the fork, as if it were stabilised by some tending force. This is not the case in the Palaeozoic Blattaria. In early Mesoblattinidae the regularity of venation may not occur in the apical parts of the wing and in the uppermost branch of M, where irregularity is present even before the M branching (late Caloblattinidae and representatives of a new family have also lost these plesiomorphic irregularities).

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[*] Caloblattinidae are autapomorphic in the wide forewing and modified habitus; the new family is characterised by a shorter ovipositor and is apomorphic in branched A1 attached to the remigial part of the wing.

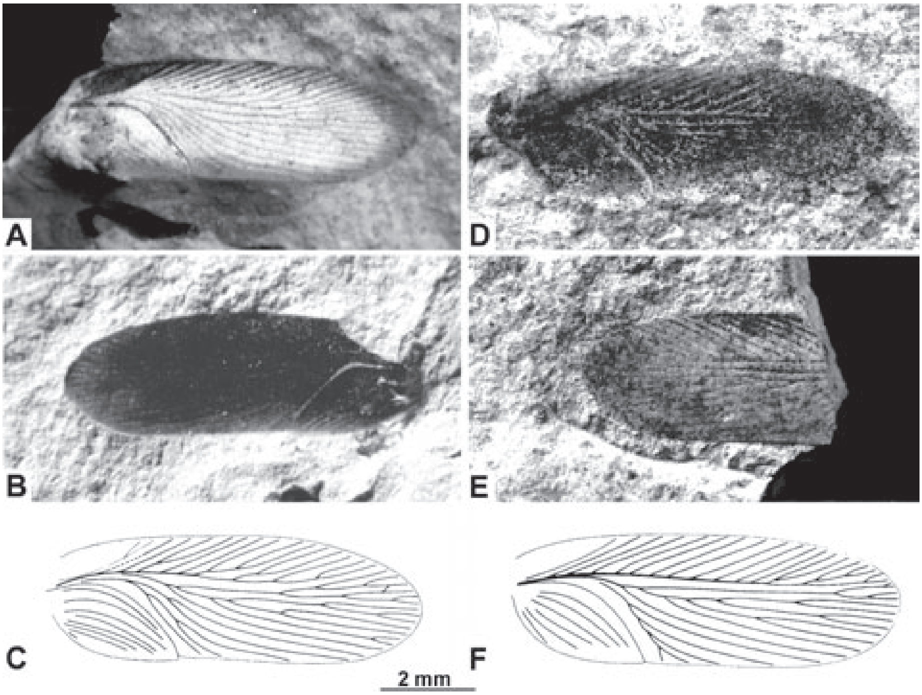

Fig. 1. *Mesoblattina protypa* Geinitz, 1880: (A–C) LGA 1942, forewing, Lower Toarcian of Grimmen; (D–F) FGWG 117/1, holotype, forewing, Lower Toarcian of Dobbertin.

Genus *Mesoblattina* Geinitz, 1880

Mesoblattina: Geinitz 1880: 519.

Type species: *Blattina* (*Mesoblattina*) *protypa* Geinitz, 1880; Lower Toarcian, Dobbertin, Germany.

Diagnosis: Forewings coriaceous, well sclerotised, with strictly parallel borders; Sc simple; R very straight, not distinguished into R and RS, with simple branches (apical branches are the exception); A not branched up to the apical third, clavus very short. Local irregularities of venation present.

Composition: Type species only.

Remarks: Other species previously assigned to *Mesoblattina* do not belong to this genus nor to the family Mesoblattinidae, and should be transferred, in most cases, into Caloblattinidae or into a new family (Vršanský, in press).

The forewing venation generally resembles *Praeblattella* Vršanský, 2003, which differs in having fully regular venation. Most closely related is apparently *Mongolblatta* Vršanský, 2004 from the Tithonian of Shar-Teg in Mongolia (synapomorphic in having coriaceous forewings) which differs in having regular venation and tuberculated anal veins (apomorphies).

With respect to all other representatives of the family Mesoblattinidae, even the oldest known is apomorphic in having coriaceous wing membranes. A phylogenetic system of the Mesoblattinidae has been presented by Vršanský (2003).

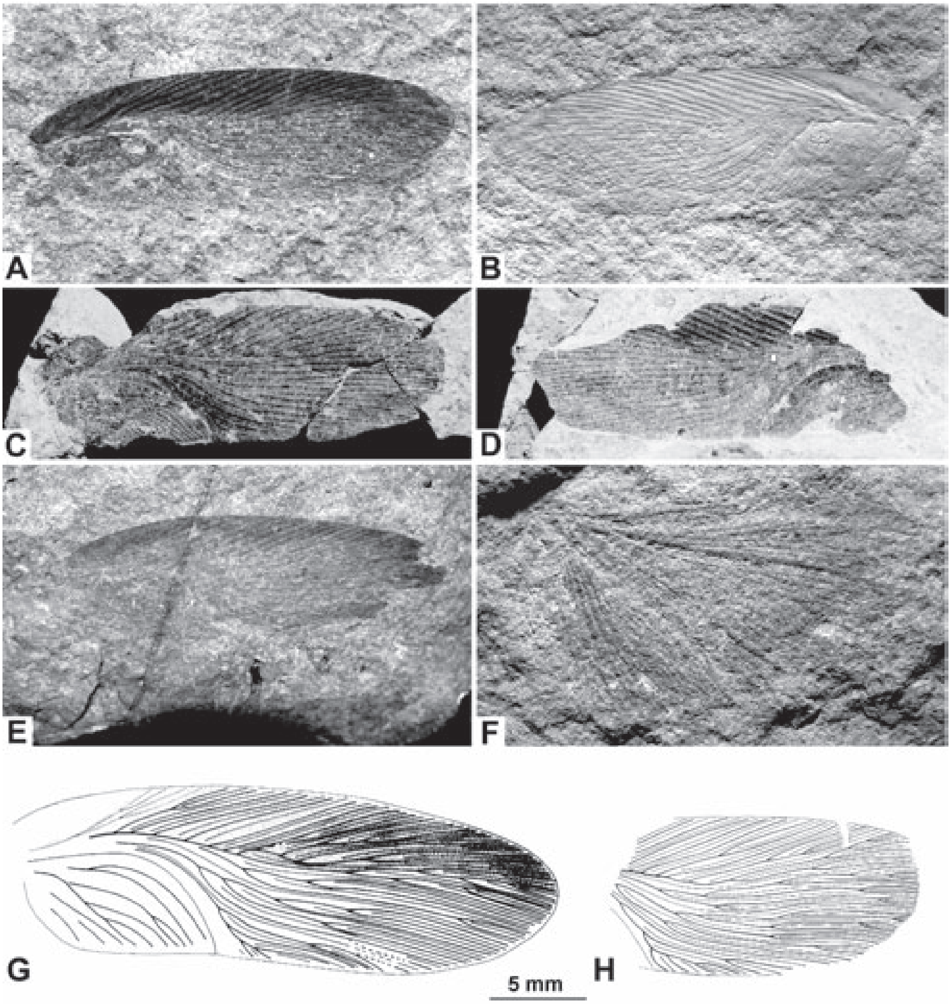

Fig. 2. *Caloblattina mathildae* (Geinitz, 1883): (A, B, G) S 300, forewing, Lower Toarcian of Schandelah near Brunswick (B, covered with ammonium chloride); (C–D) LDA 702, forewing, Lower Toarcian of Dobbertin; (E) G 402-8, holotype of *Palmoblattina gottingensis* Bode, 1953, forewing, Lower Toarcian of Hondelage near Brunswick; (F) G 402-10, holotype of *Polyphleboblatta tenuis* Bode, 1953, hindwing, Lower Toarcian of Hondelage near Brunswick; (H) FGWG 118/1, holotype of *Blattina mathildae* Geinitz, 1883, Lower Toarcian of Dobbertin.

Mesoblattina protypa (Geinitz, 1880)

Fig. 1

Blattina (*Mesoblattina*) *protypa*: Geinitz 1880: 519, fig. 1 [Fw, FGWG 117/1].
Mesoblattina protypa (Geinitz): Handlirsch 1906–08: 428, pl. 40, fig. 19.

Diagnosis: Sclerotised forewings with length about 8 mm; total number of veins at margin (excluding 6–10 A) about 38.

Description: Clavus very short, ending in basal fourth of wing, with fewer than 12 branches. Cu with 5 parallel veins and possibly one additional basal connection to margin, reaching wing apex. M rich, with about 12 branches, most of which in anterior part; R with 14–18 and possibly more branches. Sc poorly branched.

Holotype (examined): FGWG 117/1, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined: Grimmen: LGA 1320, LGA 1942; Dobbertin: FGWG 219(1), LDA 595, LDA 1086; Mistelgau: M 29, M 73 (all forewings).

Remarks: The crossvein-like fusion of radial veins at the very apex of the wing in the specimen LGA 1942 (Fig. 1E) is an unusual character and has no taxonomic value. Generally, vein fusions are more frequent in the material from Grimmen. This might have been caused by conditions of destabilised ecosystems (Vršanský 2005) within the islands, where the numerous fossils have been found.

Family Caloblattinidae Vršanský & Ansorge in Vršanský, 2000

Type genus: *Caloblattina* Handlirsch, 1906.

Composition: *Aktassoblatta* Vishniakova, 1971; *Asioblatta* Vishniakova, 1968; *Etapia* Vishniakova, 1983; *Euryblattula* Martynov, 1937; *Fusiblatta* Hong, 1980; *Ijablatta* Vishniakova, 1983; *Itchetuja* Vishniakova, 1983; *Kemerowia* Vishniakova, 1983; *Samaroblatta* Tillyard, 1919; *Samaroblattula* Martynov, 1937; *Sogdoblatta* Martynov, 1937; *Soliblatta* Lin, 1986; *Taublatta* Martynov, 1937; *Taublattopsis* Vishniakova, 1985; *Thuringoblatta* Kuhn, 1938, and probably some other insufficiently known genera.

Occurrence: Late Triassic to Late Cretaceous. The latest known representatives are from the Late Cretaceous of Siberia (unpublished material).

Genus *Caloblattina* Handlirsch, 1906

Caloblattina: Handlirsch 1906–08: 430.
Pachyneuroblattina: Handlirsch 1906–08: 433. **Syn. n.**
Apistoblattula: Bode 1953: 115. **Syn. n.**
Strebloblattula: Bode 1953: 116. **Syn. n.**
Palmoblattina: Bode 1953: 116. **Syn. n.**
Macroblattina: Bode 1953: 118. **Syn. n.**
Polyphleboblatta: Bode 1953: 120. **Syn. n.**

Type species: *Blattina mathildae* Geinitz, 1883; Lower Toarcian, Dobbertin, Germany.

Caloblattina mathildae (Geinitz, 1883)

Fig. 2

Blattina mathildae: Geinitz 1883: 29, pl. 6, fig. 1 [Fw, holotype FGWG 118/1, examined].
Caloblattina mathildae (Geinitz): Handlirsch 1906–08: 430, pl. 40, fig. 21.
Pachyneuroblattina rigida: Handlirsch 1906–08: 433, pl. 40, fig. 34 [Fw, holotype FGWG 122/13, examined]. **Syn. n.**
Apistoblattula convexa: Bode 1953: 115, pl. 5, fig. 94 [Fw, holotype Hi 1, examined]. **Syn. n.**
Strebloblattula beienrodensis: Bode 1953: 116, pl. 5, fig. 95 [Fw, SNM W 12]. **Syn. n.**
Palmoblattina gottingensis: Bode 1953: 117, pl. 5, fig. 96 [Fw, holotype G 402-8, examined]. **Syn. n.**
Macroblattina elegans: Bode 1953: 119, pl. 6, fig. 98 [Fw, SNM B 47]. **Syn. n.**
Polyphleboblatta tenuis: Bode 1953: 121, pl. 6, fig. 101 [Hw, holotype G 402-10, examined]. **Syn. n.**
Mesoblattina (?) *grandis*: Bode 1953: 125, pl. 6, fig. 99 [Hw, Cl 106]. **Syn. n.**

Diagnosis: Large species with rich venation and intercalaries that are visible even in poorly preserved material. Total number of veins about 65–75; forewing length about 25 mm; membrane heavily sclerotised.

Description: Forewing 23–30 mm long. Sc richly branched; R with 12–21 and possibly more branches; M with 9–20 veins; Cu with 11 to 22 veins. Clavus with rich venation; A branched, with about 18 branchelets at the margin. Clavus reaching basal third of wing.

Holotype (examined): FGWG 118/1, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined besides the holotypes mentioned in the synonymy list: Dobbertin, LDA 702; Schandelah, S 300.

Remarks: *C. mathildae* is generally a rare species, which is absent from the rich oryctocoenosis of Grimmen. Since there are no taphonomic reasons to explain its absence, it can only be supposed that *C. mathildae* did not live in the source area of the Grimmen insects.

Although forewings of this species have never been found in association with corresponding hindwings, *Polyphleboblatta tenuis* and *Mesoblattina* (?) *grandis*, being 23 mm long, fit well to the forewing size and are regarded as synonyms of *C. mathildae*.

?Raphidiomimidae Vishniakova, 1973

Genus *Liadoblattina* Handlirsch, 1906

Liadoblattina: Handlirsch 1906–08: 428.
Mesoblattopsis: Handlirsch 1906–08: 428. **Syn. n.**
Ptyctoblattina: Bode 1953: 121. **Syn. n.**
Trirhabdoblattina: Bode 1953: 118. **Syn. n.**

Type species: *Mesoblattina blakei* Scudder, 1886; Lower Toarcian, Alderton, England.

Liadoblattina blakei (Scudder, 1886)

Figs 3, 4

Mesoblattina blakei: Scudder 1886: 452, pl. 46, fig. 12 [Fw, holotype NHML I. 3574, examined].
Mesoblattina bensoni: Scudder 1886: 453, pl. 46, fig 17 [Fw, holotype NHML I. 3562, examined]. **Syn. n.**
Mesoblattopsis bensoni (Scudder): Handlirsch 1906–08: 428, pl. 40, fig. 12.
Liadoblattina blakei (Scudder): Handlirsch 1906–08: 428, pl. 40, fig. 17.
(?*Mesoblattina*) *zirkelii*: Handlirsch 1906–08: 435, pl. 40, fig. 39 [Hw, holotype FGWG 121/6, examined]. **Syn. n.**
(?*Mesoblattina*) *polyneura*: Handlirsch 1939: 64, pl. 5, fig. 92 [Hw, holotype FGWG 123/33, examined]. **Syn. n.**
Trirhabdoblattina borealis: Bode 1953: 118, pl. 5, fig. 97 [Fw, SNM B 120]. **Syn. n.**
Ptyctoblattina acuteplicata: Bode 1953: 122, pl. 6, fig. 102 [Hw, SNM W 49]. **Syn. n.**
Ptyctoblattina completa: Bode 1953: 123, pl. 6, fig. 103 [Hw, Hi 9]. **Syn. n.**

Diagnosis: Medium sized, with both wings coloured. Forewings elongated, as much as 3 times as long as wide (length ca. 20 mm). Clavus more than twice as long as wide.

Description: Wings membranous, with distinct coloration. Forewing with simple or weakly branched Sc and narrow costal space; gently curved R with about 15 branches, with M and Cu system developed to same degree (together with some 15 veins); rich A (at or above 10). Numerous cross-veins joined in intercalaries. Diagonal kink present in anal field.

Hindwing with simple Sc, R divided into R1 and RS (10–20 veins); M with up to 5 or more branches; Cu rich with at least 8 veins. A1 reduced compared to other related species, with 2 branches and several blind branches.

Holotype (examined): NHML I. 3574, isolated forewing. ENGLAND: *Gloucesteshire*: Alderton; Upper Lias.

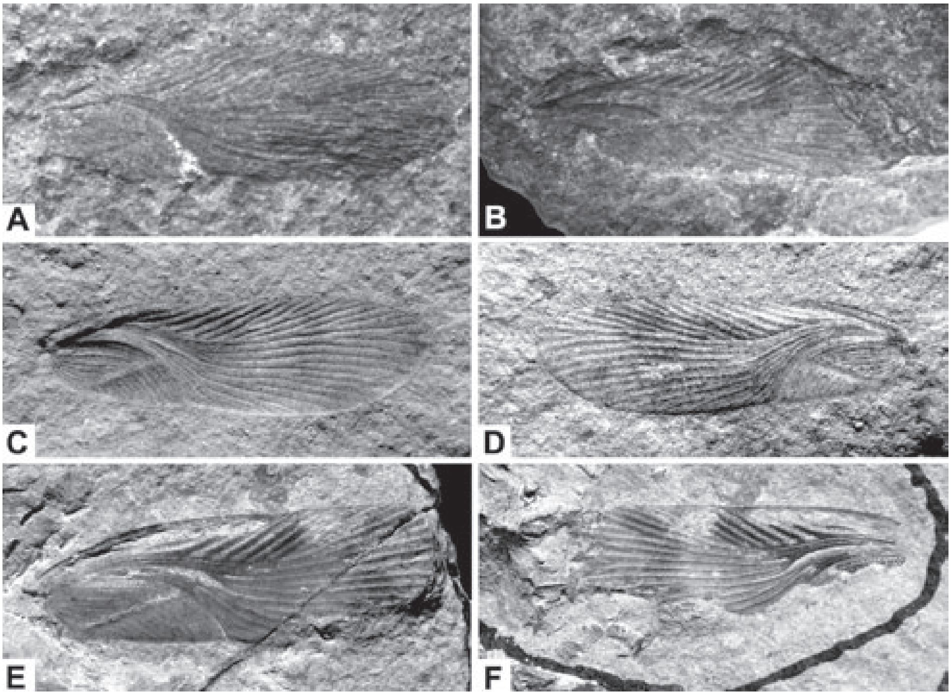

Fig. 3. *Liadoblattina blakei* (Scudder, 1886), photographs of specimens: (A) NHML I. 3562 holotype of *Mesoblattopsis bensoni* (Scudder, 1886), forewing, Upper Lias of Dumbleton, Gloucestershire, England; (B) NHML I. 3574, holotype of *Mesoblattina blakei* Scudder, 1886, Upper Lias of Alderton, Gloucestershire, England; (C–D) FGWG 223, forewing, Lower Toarcian of Dobbertin; (E–F) LDA 336, forewing, Lower Toarcian of Dobbertin.

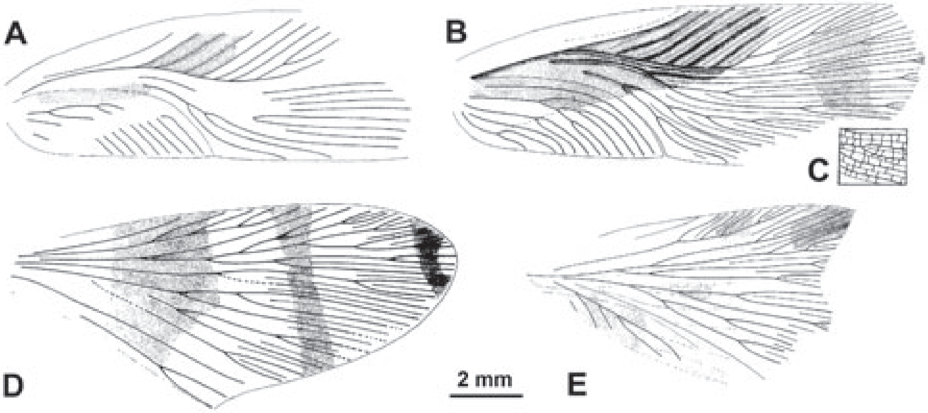

Fig. 4. *Liadoblattina blakei* (Scudder, 1886), details of wing venation: (A) NHML I. 3574, holotype of *Mesoblattina blakei* Scudder, 1886, Upper Lias of Alderton, Gloucestershire, England; (B, C) LDA 336, forewing, Lower Toarcian of Dobbertin (C, detail of intercalary veins); (D) FGWG 121/6, holotype of *Mesoblattina zirkelii* Handlirsch, 1906, hindwing, Lower Toarcian of Dobbertin; (E) FGWG 123/33, holotype of ?*Mesoblattina polyneura* Handlirsch, 1939, hindwing, Lower Toarcian of Dobbertin.

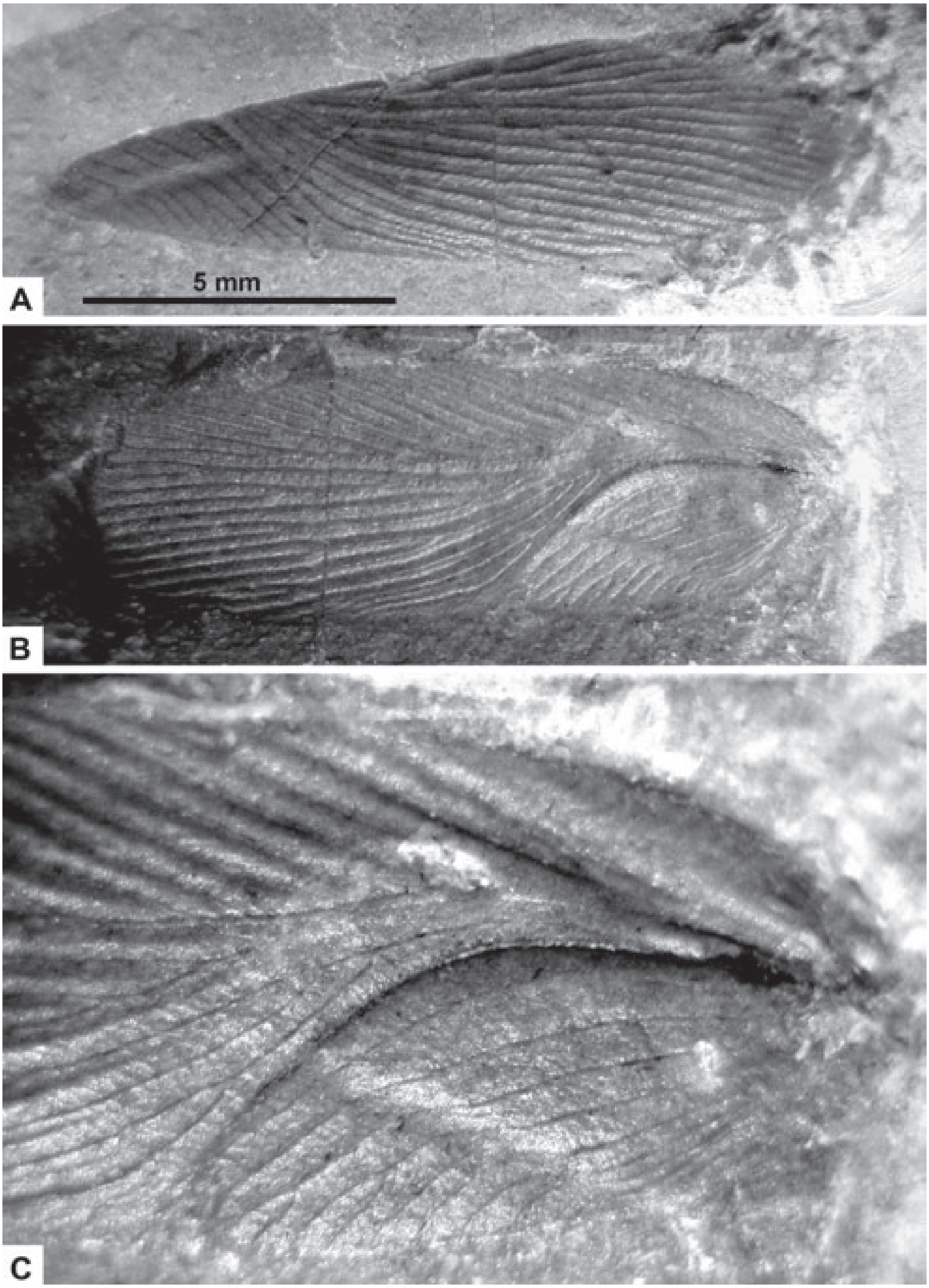

Fig. 5. *Rhipidoblattina geikiei* (Scudder, 1886), holotype NHML I. 10620, I. 11949, forewing, Lower Lias of Browns Wood, Moreton Bagot, Warwickshire, England: (A, B) part and counterpart, (C) clavus at higher magnification.

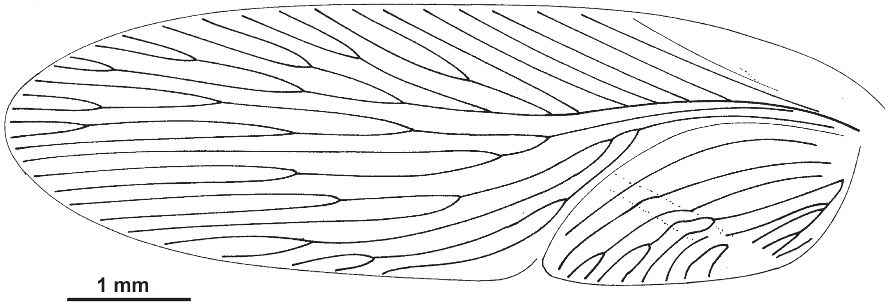

Fig. 6. *Rhipidoblattina geikiei* (Scudder, 1886), holotype, details of forewing venation.

Additional material besides the holotypes mentioned in the synonymy list examined: Dobbertin, Fw LDA 336, FGWG 223 (2); Schandelah, Fw S3-14; Holzmaden H 5, H 29, forewings.

Remarks: A1 in the hindwing seems to be formed similarly to that in Blattulidae. The taxon appears to be rather advanced, probably with actively flying individuals. Although never found associated with forewings, it is supposed that the similarly coloured hindwings, listed in the above synonymy, represent hindwings of *Liadoblattina blakei*. With a length of about 15 mm they fit well to the forewing size.

The coloration could serve as disruptive markings against visually adept predators (see Jarzembowski 1994).

Caloblattinoidea fam. n.
Genus *Rhipidoblattina* Handlirsch, 1906
Rhipidoblattina geikiei (Scudder, 1886)
Figs 5, 6

Mesoblattina geikiei: Scudder 1886: 454, pl. 46, fig. 9.
Rhipidoblattina geikiei (Scudder): Handlirsch 1906–08: 429, pl. 40, fig. 20; 1939: 57, pl. 4, fig. 72.

Diagnosis: Forewing length 13.7 mm. Total number of veins at margin about 45–50. Clavus short.

Description: Wing margins more or less parallel; venation regular with reticulations between veins. Sc field shorter than clavus, with Sc 2- or possibly 3-branched. R slightly concave with most branches simple, rarely tertiary branched, with 16 veins at margin. M rich with 9 branches; Cu expanded, with 8 branches. Faint intercalaries present (Fig. 5C). Clavus comparatively short with 12 or 13 anal veins that are branched (A1–2 simple) with diagonal kink.

Holotype (examined): Isolated forewing, part and counterpart, NHML I. 10620, I. 11949. ENGLAND: *Warwickshire*: Browns Wood, Moreton Bagot; Lower Lias.

Blattaria *incertae familiae*
Genus *Eublattula* Handlirsch, 1939
Eublattula crassivena Handlirsch, 1939
Fig. 7

Eublattula crassivena: Handlirsch 1939: 63, pl. 5, fig. 91.

Diagnosis: Forewing more than 10 mm long, with thick branches and deeply curved R not reaching wing apex. Clavus with diagonal kink.

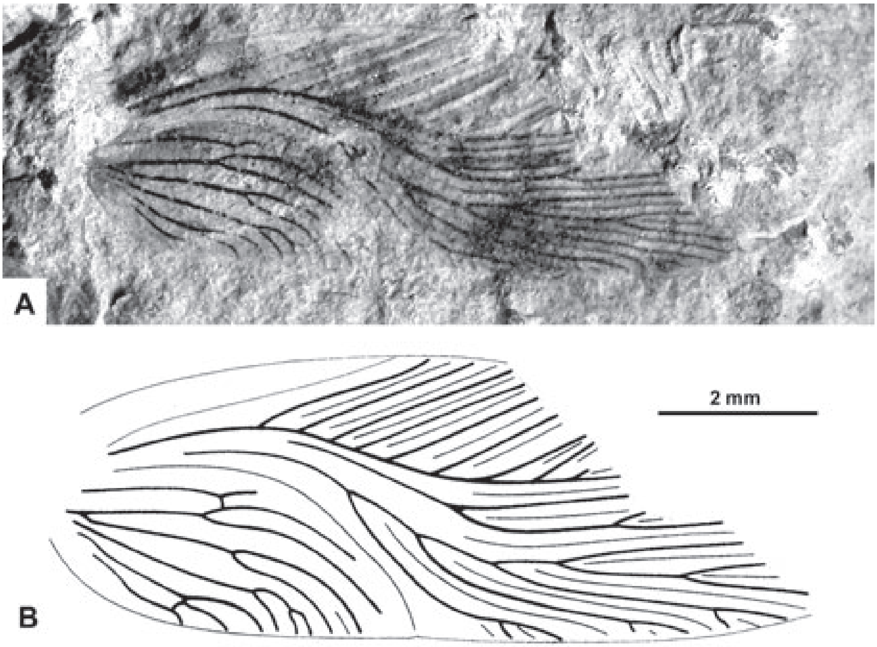

Fig. 7. *Eublattula crassivena* Handlirsch, 1939, holotype FGWG 123/32, Lower Toarcian of Dobbertin: (A) photograph of specimen, (B) details of venation.

Description: Wing with very strong venation, 11–13 mm long (distal part of wing broken), kinked clavus overlapping basal third of wing, with about 11 veins and abundant fusions; Cu expanded (6–10 veins), almost reaching wing apex. M reduced to several branches. R curved with about 10 branches. Sc simple, forked.

Holotype (examined): FGWG 123/32, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine “Green Series” clay, Lower Toarcian, *exaratum* Subzone.

Remarks: According to the vein branchings, the taxon seems to be a stem group member of the Blattulidae, or to belong to the Liberiblattinidae Vršanský, 2002.

Superfamily ?Polyphagoidea Walker, 1868

Family Blattulidae Vishniakova, 1982

Genus *Blattula* Handlirsch, 1906

Blattula: Handlirsch 1906–08: 431.
Mesoblattula: Handlirsch 1906–08: 430. **Syn. n.**
Parablattula: Handlirsch 1920: 191. **Syn. n.**
Peloblattula: Handlirsch 1939: 60. **Syn. n.**
Metablattula Handlirsch 1939: 61. **Syn. n.**
Chiloblattula: Handlirsch 1939: 61. **Syn. n.**
Ectinoblattula: Handlirsch 1939: 62. **Syn. n.**
Englyptoblatta: Bode 1953: 119. **Syn. n.**

Type species: *Blattina dobbertinensis* Geinitz, 1884 (designated by Becker-Migdisova 1962: 103) is now considered a junior synonym of *Blattula langfeldti* (Geinitz, 1880).

Remarks: Although the name *Mesoblattula* Handlirsch, 1906 has page priority over *Blattula* Handlirsch, 1906, we use the right of the first reviser to treat the name

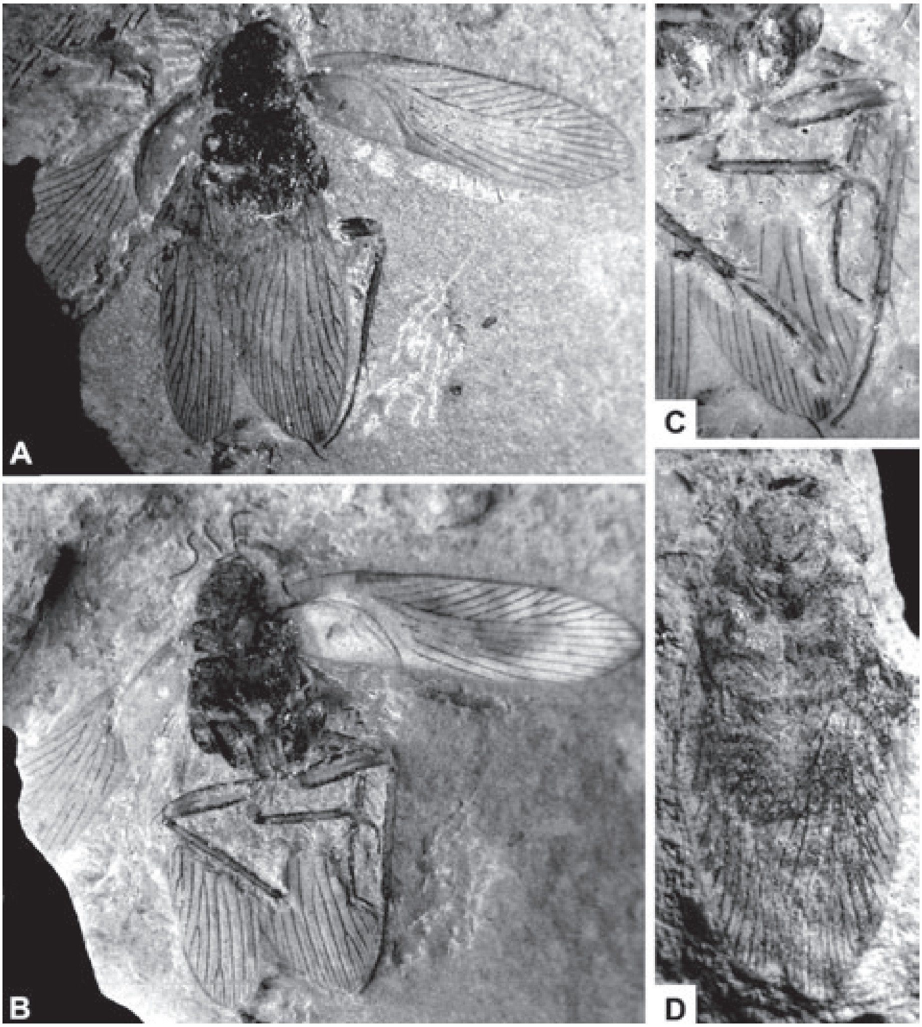

Fig. 8. *Blattula langfeldti* (Geinitz, 1880): (A–C) LGA 1820, Lower Toarcian of Grimmen: (A) total before preparation of legs, (B) after preparation of legs and antennae, (C) details of legs; (D) LDA 96, Lower Toarcian of Dobbertin.

Mesoblattula as a junior subjective synonym of *Blattula*. *Blattula* is very similar in wing venation to the mainly Lower Cretaceous *Elisama* Giebel, 1856. The most striking difference is a dark macula in *Elisama* forewings.

Blattula langfeldti (Geinitz, 1880)

Figs 8–15

Blattina langfeldti: Geinitz 1880: 521, fig. 3 [Fw, holotype FGWG 117/20, examined].

Blattina nana: Geinitz 1883: 30, pl. 22, fig. 2 [Hw, holotype FGWG 118/3, examined]. **Syn. n.**

Blattina (*Mesoblattina*) *dobbertinensis*: Geinitz 1884: 570, pl. 13, fig. 1 [Fw, holotype FGWG 119/2, examined]. **Syn. n.**

Blattina incerta: Geinitz 1884: 571, pl. 13, fig. 2 [Hw, holotype FGWG 119/2, examined]. **Syn. n.**

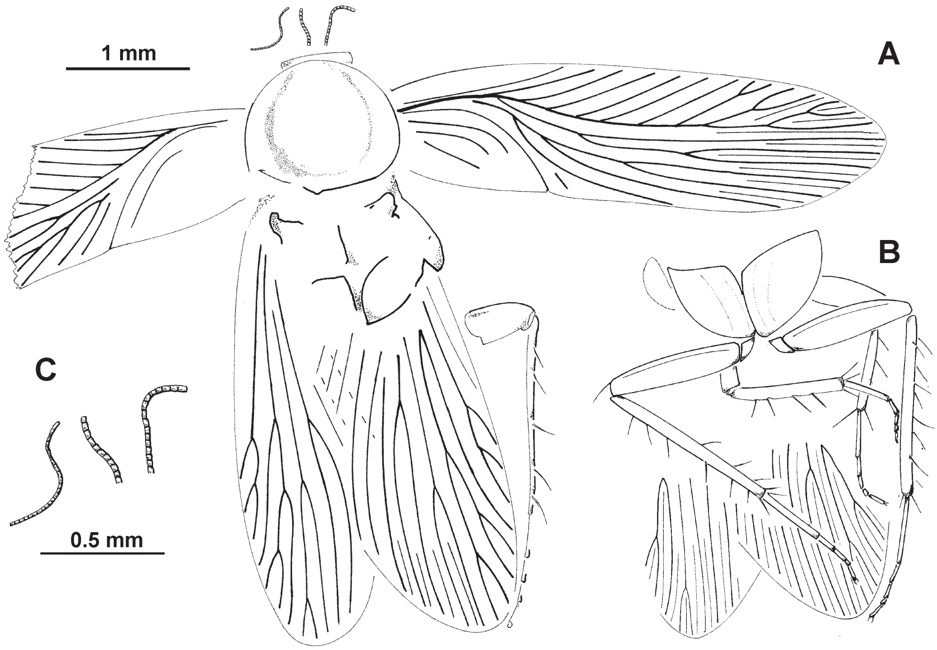

Fig. 9. *Blattula langfeldti* (Geinitz, 1880), LGA 1820, Lower Toarcian of Grimmen: (A) details of specimen before preparation of legs, (B) details of legs after preparation, (C) details of antennae.

Dipluroblattina scudderi: Geinitz 1887: 200, pl. 5, fig. 7 [Fw, holotype FGWG 120/2, examined]. **Syn. n.**
Ctenoblattina langfeldti (Geinitz): Scudder 1886: 443.
Mesoblattina dobbertinensis (Geinitz): Scudder 1886: 455.
Mesoblattula dobbertiniana: Handlirsch 1906–08: 430, pl. 40, fig. 23 [Fw, holotype FGWG 122/103, examined]. **Syn. n.**
Mesoblattula geinitziana: Handlirsch 1906–08: 430, pl. 40, fig. 24 [Fw, holotype FGWG 122/10-11, examined]. **Syn. n.**
Blattula dobbertinensis (Geinitz): Handlirsch 1906–08: 431, pl. 40, fig. 25.
Blattula langfeldti (Geinitz): Handlirsch 1906–08: 431, pl. 40, figs 26, 27.
Blattula ancilla: Handlirsch 1906–08: 431, pl. 40, fig. 28 [Fw, holotype FGWG 122/12, examined]. **Syn. n.**
Blattula geinitzi: Handlirsch 1906–08: 432, pl. 40, fig. 29 [Fw, probably lost]. **Syn. n.**
Battula scudderi (Geinitz): Handlirsch 1906–08: 432, pl. 40, fig. 30.
?*Blattula incerta* (Geinitz): Handlirsch 1906–08: 432, pl. 40, fig. 31.
?*Blattula debilis*: Handlirsch 1906–08: 433, pl. 40, fig. 32. **Syn. n.**
?*Blattula pusillima*: Handlirsch 1906–08: 433, pl. 40, fig. 33 [Hw, holotype FGWG 122/250, examined]. **Syn. n.**
(?*Mesoblattina*) *nana* (Geinitz): Handlirsch 1906–08: 435, pl. 40, fig. 38.
Parablattula reticulata: Handlirsch 1920: 191, fig. 153 [Fw, holotype FGWG 123/26, examined]; 1939: 61, pl. 5, fig. 83. **Syn. n.**
?*Mesoblattula ala*: Handlirsch 1939: 58, pl. 4, fig. 74 [Hw, holotype FGWG 123/45, examined]. **Syn. n.**
Blattula riparia: Handlirsch 1939: 58, pl. 4, fig. 75 [Fw, holotype FGWG 123/20, examined]. **Syn. n.**
Blattula intercalata: Handlirsch 1939: 58, pl. 4, fig. 76 [Fw, holotype FGWG 123/21, examined]. **Syn. n.**
Blattula brunneri: Handlirsch 1939: 59, pl. 5, fig. 77 [Fw, holotype FGWG 123/22, examined]. **Syn. n.**
?*Blattula vicina*: Handlirsch 1939: 59, pl. 5, fig. 79 [Fw, holotype FGWG 123/23, examined]. **Syn. n.**
?*Blattula acutipennis*: Handlirsch 1939: 59, pl. 5, fig. 80 [Hw, NHMW 1984/33/11]. **Syn. n.**
Peloblattula oligoneura: Handlirsch 1939: 60, pl. 5, fig. 81 [Fw, holotype FGWG 123/24, examined]. **Syn. n.**
Parablattula simplicissima: Handlirsch 1939: 60, pl. 5 fig. 82 [Fw, holotype FGWG 123/25, examined; counterpart NHMW 1984/33/12]. **Syn. n.**
Metablattula lipomena: Handlirsch 1939: 61, pl. 5, fig. 84 [Fw, holotype FGWG 123/27, examined]. **Syn. n.**
Chiloblattula simplex: Handlirsch 1939: 61, pl. 5, fig. 85 [Fw, holotype FGWG 123/28, examined]. **Syn. n.**
?*Chiloblattula subcostalis*: Handlirsch 1939: 62 [Hw, holotype FGWG 123/29, examined]. **Syn. n.**

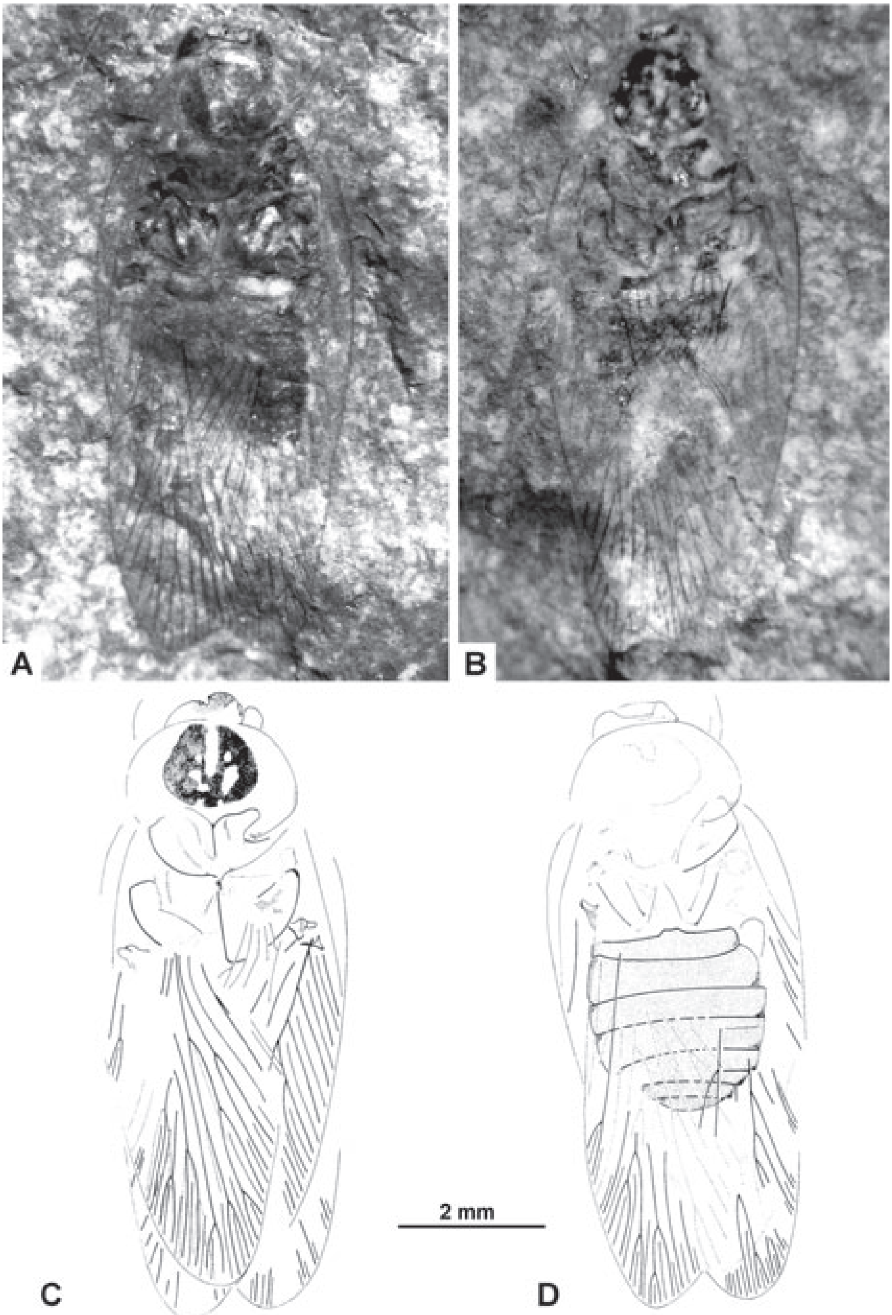

Fig. 10. *Blattula langfeldti* (Geinitz, 1880), LGA 888/1-2, Lower Toarcian of Grimmen: (A, B) photographs of part and counterpart, (C, D) details of body structures.

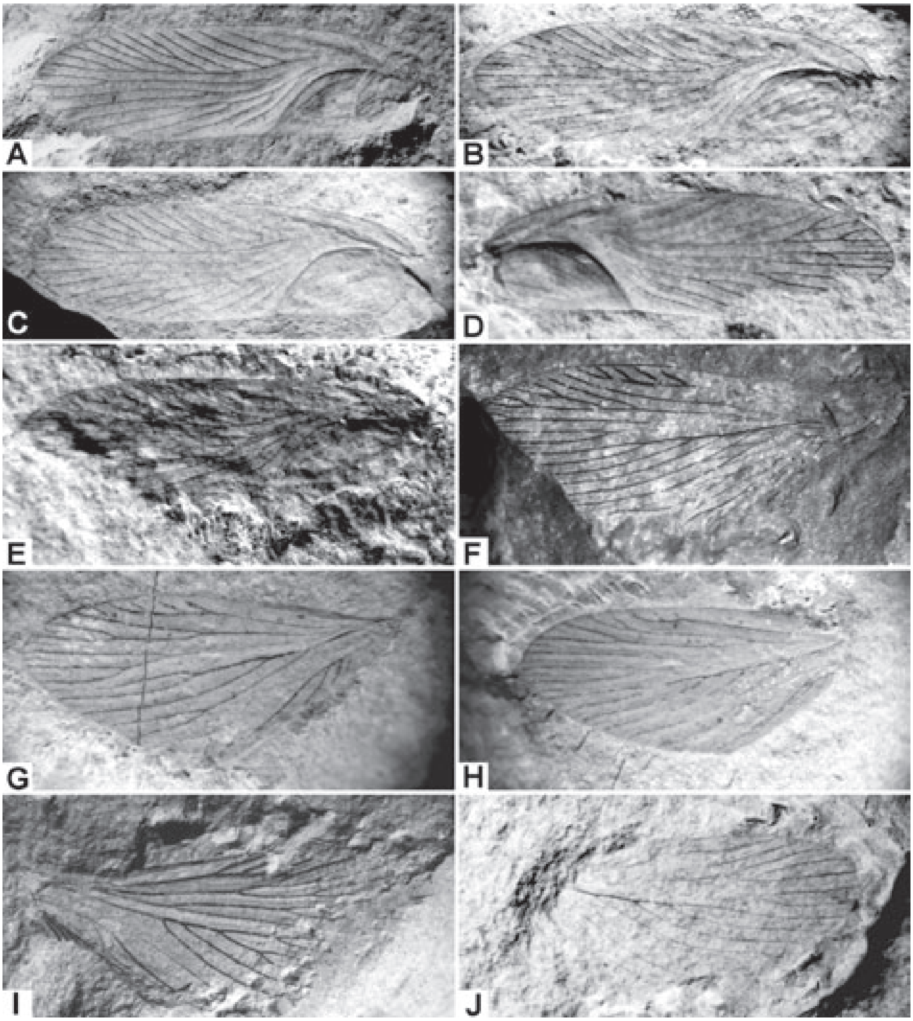

Fig. 11. *Blattula langfeldti* (Geinitz, 1880): (A) FGWG 123/26, forewing, holotype of *Parablattula reticulata* Handlirsch, 1939, Dobbertin; (B) LDA 7, forewing, Dobbertin; (C) LDA 66, forewing, Dobbertin; (D) LGA 2356, forewing, Grimmen; (E) LDA 586, forewing, Dobbertin; (F) LGA 96, hindwing, Grimmen; (G) LGA 1275, hindwing, Grimmen; (H) LGA 2507, hindwing, Grimmen; (I) LGA 380, hindwing, Grimmen; (J) LDA 85, hindwing, Dobbertin.

?*Chiloblattula longipennis*: Handlirsch 1939: 62, pl. 5, fig. 86 [Hw, holotype FGWG 123/30, examined]. **Syn. n.**
Ectinoblattula medialis: Handlirsch 1939: 63, pl. 5, fig. 90 [Fw, holotype FGWG 123/57, examined]. **Syn. n.**
Blattula hattorfensis: Bode 1953: 114, pl. 5, fig. 93 [Fw, SMN W 13]. **Syn. n.**
Englyptoblatta elegantula: Bode 1953: 120, pl. 6, fig. 100 [Fw, SNM W 9/11]. **Syn. n.**
Elisama langfeldti (Geinitz): Ansorge 2003: 296, fig. 2B.
Blattula langfeldti (Geinitz): Ansorge 2004: 782, fig. 2.

Diagnosis: Forewing: length 6.5–9 mm; Sc 1, R 8–14, M 2–7, Cu 4–10, A 5–12. Hindwing: length 6.5–7.5 mm; Sc 1, R 3–4+3–5, M 2–3, Cu 6–8.

Description: Pronotum ovoid in shape, transverse, with distinct coloration. Forewing length 6.5–9 mm, width about 2.3 mm; Sc simple, rarely with some weak lateral

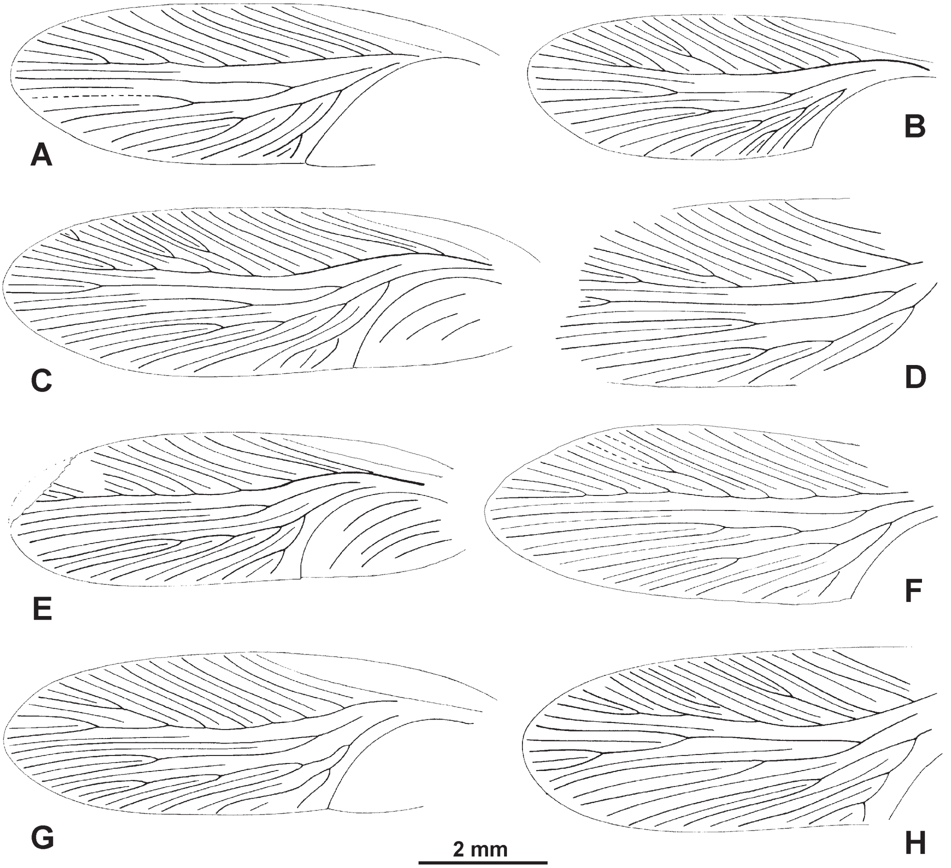

Fig. 12. *Blattula langfeldti* (Geinitz, 1880), details of venation of forewings, Lower Toarcian of Dobbertin and Grimmen: (A) FGWG 122/12, holotype of *Blattula ancilla* Handlirsch, 1906; (B) LGA 880; (C) FGWG 123/26, holotype of *Parablattula reticulata* Handlirsch, 1920; (D) FGWG 123/25, holotype of *Parablattula simplicissima* Handlirsch 1939; (E) FGWG 123/28, holotype of *Chiloblattula simplex* Handlirsch, 1939; (F) FGWG 123/27, holotype of *Metablattula lipomena* Handlirsch, 1939; (G) FGWG 119/2, holotype of *Blattula dobbertinensis* (Geinitz, 1884); (H) FGWG 122/103, holotype of *Mesoblattula dobbertiniana* Handlirsch, 1906.

branchlets; R with 8–14 veins; M with 2–7 branches; Cu with 4–10 branches. A reticulate, with 5–12 veins reaching margin, veins in clavus may be reticulate. Hindwing length 6.5–7.5 mm with Sc simple; R divided near base into R with 3–4 veins and RS with 3–5 veins; M with 2 or 3 branches; CuA with 6–8 veins. Legs thin, with sparse, long and thin spines.

Holotype (examined): FGWG 117/20, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine “Green Series” clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined: Besides the re-studied holotypes described by Geinitz and Handlirsch from the Lower Toarcian of Dobbertin and listed in the synonymy, the following additional material is in Ansorge’s collection. Hindwings: LDA 40; 76; 85; 86; 109; 455; 485; 594/3; 660/1, 2; 593/3; LGA 86; 96; 275; 331/1, 2; 380; 425; 579; 594; 888; 893; 1077; 1201; 1275; 1372; 1529; 1578; 1739; 1820; 2169. Forewings: LDA 7, 66; 169; 240; 145; 254; 289; 326; 348; 581; 586; 629; 611; 798; 869; 910; 1017; 2196; LGA 13; 118; 154; 880; 1328; 1435; 1519; 1842; 1887; 1926; 2006; 2015; 2196; 2356, S 137; 139. Complete specimens:

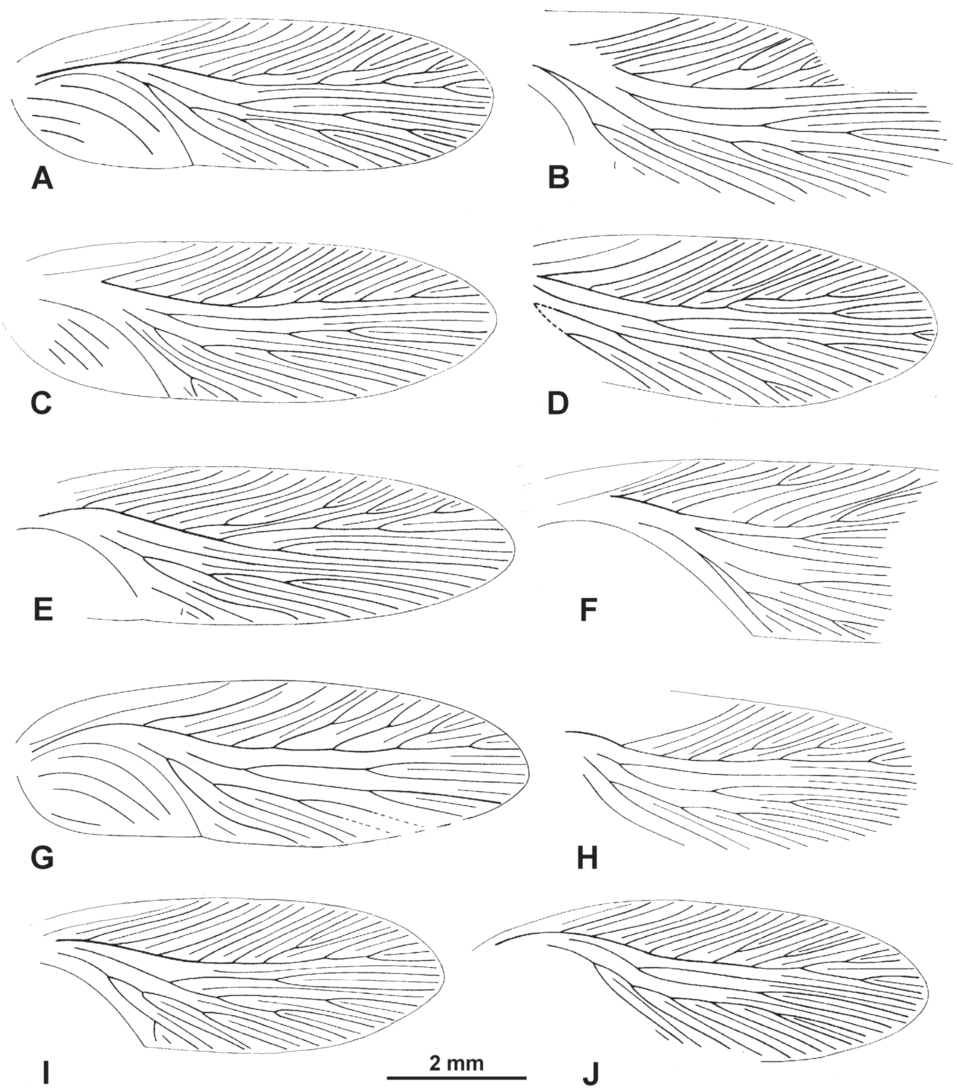

Fig. 13. *Blattula langfeldti* (Geinitz, 1880), details of venation of forewings, Lower Toarcian of Dobbertin, Grimmen (LGA 2356) and Schandelah (S 139): (A) FGWG 123/21, holotype of *Blattula intercalata* Handlirsch, 1939; (B) FGWG 120/2, holotype of *Dipluroblattina scudderi* Geinitz, 1887; (C) FGWG 123/20, holotype of *Blattula riparia* Handlirsch, 1939; (D) FGWG 117/20, holotype of *Blattina langfeldti* Geinitz, 1880; (E) FGWG 123/57, holotype of *Ectinoblattula medialis* Handlirsch, 1939; (F) FGWG 122/10-11, holotype of *Mesoblattula geinitziana* Handlirsch, 1906; (G) LGA 2356; (H) S 139; (I) FGWG 123/24, holotype of *Peloblattula oligoneura* Handlirsch, 1939; (J) FGWG 123/22, holotype of *Blattula brunneri* Handlirsch, 1939.

LDA 96; LGA 888; 1820. Two species described by Bode (1953) from the Lower Toarcian of Hattorf (Lower Saxony) have not been re-examined.

Note: A few complete specimens with associated fore- and hindwings allow us to determine isolated fore- and hindwings.

Variability (Tables 2, 3): Both complete specimens from Grimmen show considerable variation between the left and right wings. Sc is stable, simple in all wings. Other veins

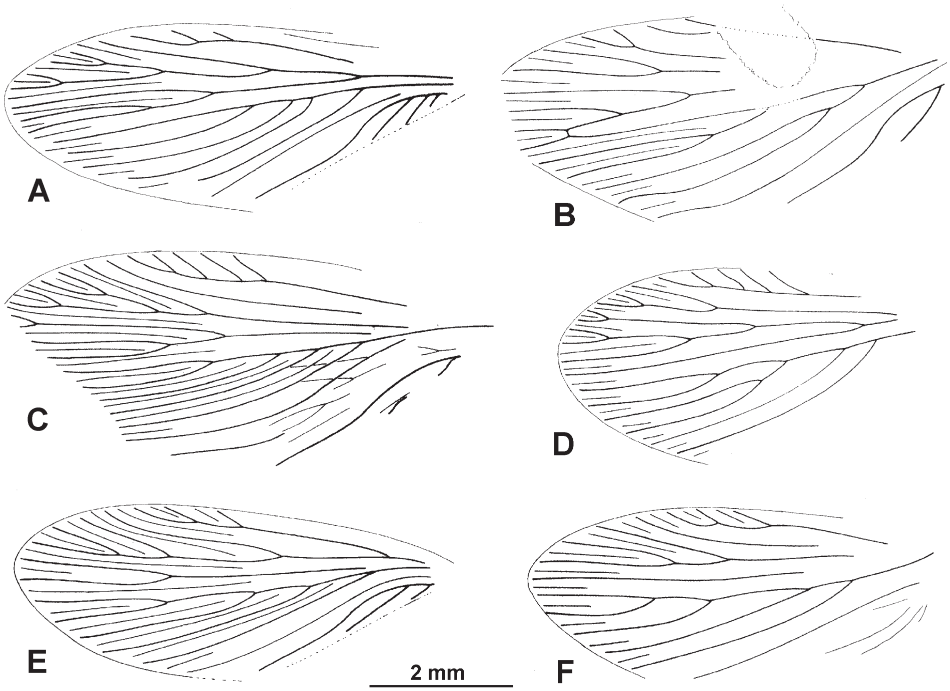

Fig. 14. *Blattula langfeldti* (Geinitz, 1880), details of venation of hindwings, Lower Toarcian of Dobbertin (FGWG) and Grimmen (LGA): (A) FGWG 123/23, holotype of ?*Blattula vicina* Handlirsch, 1939; (B) LGA 579; (C) LGA 96; (D) LGA 893; (E) FGWG 123/30, holotype of ?*Chiloblattula longipennis* Handlirsch, 1939; (F) FGWG 122/250, holotype of ?*Blattula pusillima* Handlirsch, 1906.

vary. Hindwing variation, considered as more stable, is expressed in the varying number of RS branches (4 in left wing; 5 in right wing), while R is stable in this case (3). M is 3-branched in the left wing, and 2-branched in the right wing. Unfortunately, the wings are not complete, so it is uncertain whether the Cu will compensate differences in the total vein number (6 in right wing, and evidently more than 3 in the left wing).

TABLE 2

Variability of the forewings of *Blattula langfeldti*. SUM designates the total number of all veins, except for A, at wing margin.

	size, mm	Cu	M	R	R+M	Cu+M	R+Cu	SUM
Sample size (n)	44	44	44	44	43	43	39	42
Minimum	6.4	4	1	6	11	7	12	17
Maximum	9.0	10	9	15	19	16	23	28
Median	7	6	4	11	15	10	17	22
Mode	7	6	4	11	14	9	19	22
Standard error	0.10	0.19	0.21	0.30	0.32	0.29	0.39	0.38
Standard deviation	0.63	1.23	1.40	1.96	2.05	1.90	2.44	2.47
Variance	0.40	1.52	1.95	3.85	4.19	3.61	5.98	6.09
Coefficient of variation	8.71	20.06	33.58	18.22	13.73	18.37	14.51	11.24

TABLE 3

Variability of the hindwing of *B. langfeldti*. SUM designates the total number of all veins (only remigial veins are counted; R is R1+RS) at wing margin.

	size, mm	Cu	M	R	R1	RS	R+M	Cu+M	R+Cu	SUM
Sample size	24	31	32	28	34	30	28	30	27	22
Minimum	6	5	1	4	2	2	8	6	10	14
Maximum	8	8	6	11	5	6	15	13	18	22
Median	7	6	3	7	3	4	10	9	14	17
Mode	7	6	3	7	3	4	10	9	15	18
Standard error	0.08	0.15	0.17	0.25	0.14	0.15	0.35	0.28	0.33	0.51
Standard deviation	0.38	0.85	0.98	1.32	0.82	0.83	1.84	1.53	1.73	2.39
Variance	0.14	0.72	0.97	1.74	0.67	0.69	3.37	2.35	2.98	5.73
Coefficient of variation	5.41	13.81	32.79	17.50	24.16	19.40	17.42	16.73	12.46	13.86

The variability studies of *B. langfeldti* revealed some general principles regarding the control of the cockroach wing venation development. With the increasing number of veins in a competent venational complex, the variability falls (coefficient of variation (CV) is lower). Therefore we have also analysed the dependence of the CV according to the number of veins. Results show that the CV is comparatively low in the competent venational systems (R, M, Cu), higher in neighbouring venational complexes and the highest between complexes that are not neighbouring (in the forewing of *B. langfeldti* it is low in (R+M) complex, high in (R) and (Cu); in the hindwing, the most apparent is the relatively high variability of (R+Cu) complex). That means that the control mechanisms are developed autonomically, "working best" in each venational complex (R, M, Cu) (each major branch has its own control mechanism) but these separate systems communicate with their surroundings, and influence each other (see Schneider 1977, 1978*a*).

Remarks: There is no gap in the variability of the venation which would suggest dimorphism in the flight abilities of both sexes.

Blattula dubia (Handlirsch, 1939), **comb. n.**

Fig. 16

?*Chiloblattula dubia*: Handlirsch 1939: 62, pl. 5, fig. 89.

Diagnosis: One of smallest known blattulids, with forewing length 4.5–6 mm and venation reduced to some 20 veins.

Description: Forewing with venation reduced to some 20 veins. R with about 7 veins; M with about 3; Cu with about 4. Hindwing with R1 and RS (3–5+3–5); M with 2 or 3 branches; Cu with 4–5+1 branches; A1 with at least two branches.

Holotype (examined): FGWG 123/31, isolated hindwing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined: Dobbertin, hindwing LDA 304/1; Grimmen, forewing LGA 1725.

Remarks: The species differs from *B. langfeldti* in having a rounded forewing margin and in having more reduced venation, which results from the smaller size of this species.

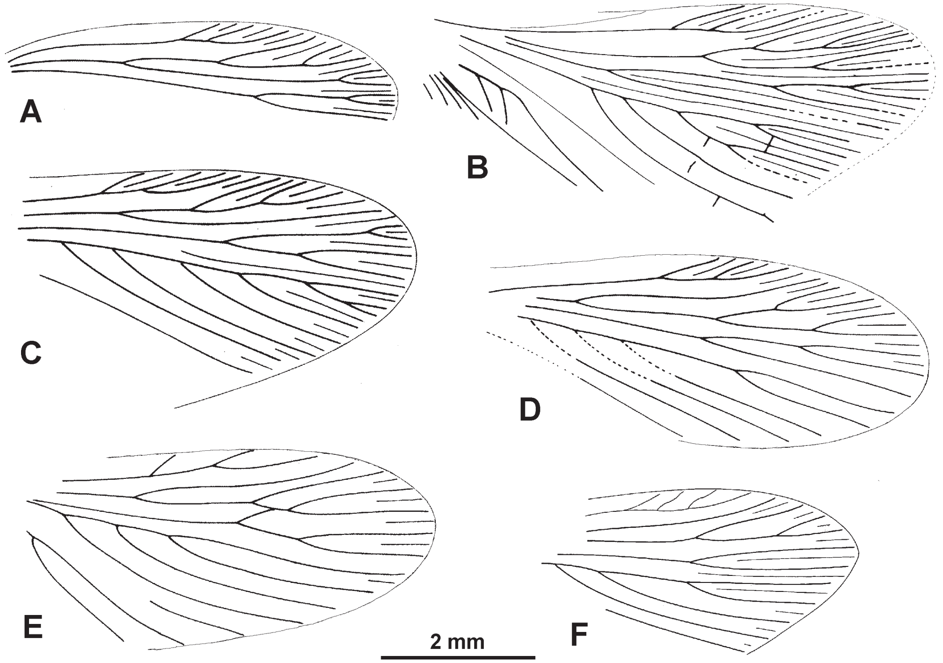

Fig. 15. *Blattula langfeldti* (Geinitz, 1880), details of venation of hindwings, Lower Toarcian of Dobbertin and Grimmen (LGA 380): (A) FGWG 123/45, holotype of ?*Mesoblattula ala* Handlirsch, 1939; (B) LGA 380; (C) FGWG 118/3, holotype of *Blattina nana* Geinitz, 1883; (D) FGWG 119/2, holotype of *Blattina incerta* Geinitz, 1884; (E) LDA 85; (F) FGWG 123/29, holotype of ?*Chiloblattula subcostalis* Handlirsch, 1939.

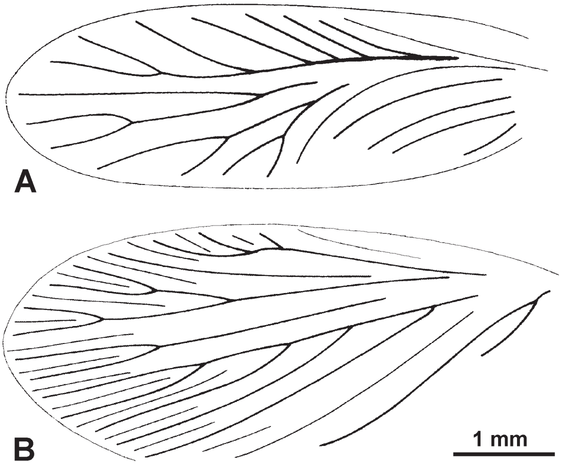

Fig 16. *Blattula dubia* (Handlirsch, 1939), wing venation: (A) LGA 1725, forewing, Lower Toarcian of Grimmen; (B) FGWG 123/31, hindwing, holotype of ?*Chiloblattula dubia* Handlirsch, 1939, Lower Toarcian of Dobbertin.

Although not found in association with a hindwing, a very small isolated forewing LGA 1725 from Grimmen most likely belongs to this species.

DISCUSSION

Cockroaches from the Lower Toarcian marine insect oryctocoenoses are mainly represented by isolated wings and wing fragments, e.g., isolated anal fields. *B. langfeldti*, the most common cockroach in Grimmen and Dobbertin, is known from three complete specimens. The record of few articulated specimens and a similar number of fore- and hindwings indicates that representatives of this species were capable fliers. In accordance with the supposed close position of the depositional realm of the Grimmen and Dobbertin insects to a shore line, we see a reason that this species is rather rare in the other localities, which were thought to have been further offshore.

The large *C. mathildae* and *L. blakei* are absent from Grimmen, which may indicate that these species did not live in the source area (islands) of the Grimmen insects. Otherwise, the composition of the insect fauna in marine oryctocoenoses is definitely controlled by taphonomic factors and it depends primarily on the distance to the shoreline.

Taxonomic work is made difficult by increasing complexity within the systematics of this order. Our observations are based on investigations of Vishniakova (1983), Schneider (1977, 1978*a*, *b*, 1980*a*, *b*, 1983, 1984), Schneider and Werneburg (1993) and ourselves. The taxonomic and systematic position of the Mesoblattinidae, differing from Caloblattinidae is now fully recognised, based on the apparent difference in size, general habitus, terminalia and venational characters.

The diversity of the studied Lower Toarcian cockroaches is low, most probably as a result of the island character within the source area. Blattulidae are represented only by two species, with *B. langfeldti* dominant (88 specimens) and with higher variability compared with the Lower Cretaceous Blattulidae of the same size and having the same number of veins. Both sexes shared a similar habitus and do not differ significantly in the size or form.

Very little is known about the niches of fossil cockroaches, but all the studied cockroaches appear to be saprophagous, although in Jurassic *Liadoblattina* from Asia, lengthening of the body and wings may suggest a predatory habit as in Upper Jurassic Raphidiomimidae Vishniakova, 1973 and in mantises (Vršanský 1999*a*, 2002).

Unlike the most common *B. langfeldti* and other representatives of the family Blattulidae, the wing structure of the largest *Caloblattina* species suggests that representatives of the species were not active fliers. Other species belonging to the Blattulidae have been found together with apparently diurnal Umenocoleidae in coprolites from Mongolia (Vršanský 2003). Thus it is likely that the most common Blattulidae were also diurnal.

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